

TEMPORAL AND SPATIAL STABILITY OF RED-TAILED HAWK TERRITORIES IN THE LUQUILLO EXPERIMENTAL FOREST, PUERTO RICO

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ABSTRACT.—We mapped Red-tailed Hawk (*Buteo jamaicensis*) territories in the Luquillo Experimental Forest (LEF) of Puerto Rico in 1998. We combined our 1998 data with that collected during previous studies of Red-tailed Hawks in the LEF to examine population numbers and spatial stability of territorial boundaries over a 26-yr period. We also investigated potential relationships between Red-tailed Hawk territory sizes and topographic and climatic factors. Mean size of 16 defended territories during 1998 was 124.3 ± 12.0 ha, which was not significantly different from our calculations of mean territory sizes derived from data collected in 1974 and 1984. Aspect and slope influenced territory size with the smallest territories having high slope and easterly aspects. Territory size was small compared to that reported for other parts of the species' range. In addition, there was remarkably little temporal change in the spatial distribution, area, and boundaries of Red-tailed Hawk territories among the study periods. Further, there was substantial boundary overlap (21–27%) between defended territories among the different study periods. The temporal stability of the spatial distribution of Red-tailed Hawk territories in the study area leads us to believe the area might be at or near saturation.

KEY WORDS: *Buteo jamaicensis; Red-tailed Hawk; Puerto Rico; spatial stability; temporal stability; territorial characteristics.*

ESTABILIDAD TEMPORAL Y ESPACIAL DE LOS TERRITORIOS DEL GAVILAN DE COLA ROJA EN EL BOSQUE EXPERIMENTAL DE LUQUILLO, PUERTO RICO.

RESUMEN.—Hicimos mapas de los territorios del gavilán de cola roja (*Buteo jamaicensis*) en el Bosque Experimental de Luquillo (BEL) en Puerto Rico en 1998. Combinamos nuestros datos de 1998 con aquellos colectados durante estudios previos con gavilanes de cola roja en el BEL para examinar los números de la población y la estabilidad espacial de los límites de los territorios en un periodo de 26 años. Además investigamos las posibles relaciones entre los tamaños de los territorios del gavilán y factores topográficos y climáticos. El tamaño medio de los 16 territorios defendidos durante 1998 fue 124.3 ± 12.0 ha, lo cual no fue significativamente diferente de nuestros cálculos del tamaño medio de los territorios a partir de datos colectados en 1974 y 1984. La cara y la pendiente influyeron en el tamaño del territorio, teniendo los territorios más pequeños altas pendientes y caras orientales. El tamaño del territorio fue pequeño comparado con los reportados para otras partes dentro del rango de la especie. Adicionalmente, hubo notablemente poco cambio temporal en la distribución espacial, área y límites de los territorios del gavilán de cola roja entre los periodos estudiados. Además hubo un traslape substancial en los límites (21–27%) en los territorios defendidos entre los diferentes perio-

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dos estudiados. La estabilidad temporal en la distribución espacial de los territorios del gavilán de cola roja en el área de estudio no lleva a creer que el área puede estar en o cerca de su saturación.

[Traducción de César Márquez]

The Red-tailed Hawk (*Buteo jamaicensis*) is possibly the most ubiquitous raptor in North America, with a distribution from Alaska and northern Canada south through most of Mexico and into Central America, and east across the West Indies (Snyder and Snyder 1991). It occupies a diversity of ecotypes, but is typically considered a raptor of open country characterized by interspersed woodlots (Preston and Beane 1993). Red-tailed Hawks are primarily sit-and-wait predators, scanning open areas from elevated perch sites (Preston and Beane 1993). However, these hawks also occupy tropical forest areas (Snyder and Snyder 1991, Preston and Beane 1993). The Red-tailed Hawk population in the Luquillo Experimental Forest (LEF) of Puerto Rico is one of the densest (1.6 pairs/km²) ever reported for the species (Snyder and Snyder 1991, Preston and Beane 1993). Furthermore, Santana and Temple (1988) found the density of Red-tailed Hawks was greatest in the mountainous rain forest of the LEF and lowest in the open-country lowlands. This is intriguing because the LEF is a closed-canopy forest and quite atypical from the usual open and mixed vegetation ecotypes commonly occupied by Red-tailed Hawks (Howell et al. 1978, Preston and Beane 1993).

We mapped Red-tailed Hawk territories in the LEF study area in 1998. Here we combine our data with that collected during previous studies of these species in the LEF from 1972–75 (Snyder et al. 1987; hereafter 1970s study) and from 1981–83 (Santana and Temple 1988; hereafter 1980s study) to examine population stability and the spatial stability of territorial boundaries across three decades. We also explore potential relationships of topographic and climatic factors to territory sizes in the study area.

STUDY AREA

Our study area was an irregularly shaped 32-km² area within the Luquillo Experimental Forest (Snyder et al. 1987). The LEF is a subtropical rain forest in the Luquillo Mountains, located at the east end of the island of Puerto Rico (18°N, 65°W), and is part of the Caribbean National Forest in the U.S. Department of Agriculture National Forest system. The study area ranges from 300–1050 m in elevation and includes “tabonuco forest” (subtropical wet forest life zone), “colorado forest” (lower montane wet forest life zone), and “cloud forest” (lower montane rain forest life zone) (Ewel and Whitmore

1973). In general, as elevation increases, mean tree height, diameter, basal area, and species richness decreases, while stem density increases (Brown et al. 1983). Annually, the study area receives more than 1000 rain showers, with rainfall ranging from 354–485 cm (García-Martino et al. 1996). Temperatures at the highest elevations range from 17–20°C (García-Martino et al. 1996).

METHODS

A territory is usually considered as that area in which a resident individual or pair excludes conspecifics (Powell 2000). Red-tailed Hawks in the LEF defend their territories year-round, attacking any conspecifics that stray into their territory (Snyder et al. 1987). Observations of intraspecific encounters between neighboring Red-tailed Hawks allow mapping of territory boundaries (Janes 1984, Santana and Temple 1984, Snyder et al. 1987).

Intraspecific territorial encounters typically involve the resident Red-tailed Hawk diving from a soar or initiating a direct flapping chase. Intruders are pursued by one or both members of the resident pair to a boundary of the territory, at which point the intruder stops fleeing and both resident and intruder will circle up near each other while vocalizing. The interaction ends when both resident and intruder retreat into their respective territories, often with one individual of a pair flying above and to the rear of its mate, after which the pairs drop down into their territories, presumably near the nest area. The sequence of soaring residents chasing intruding neighbors to a boundary, then circling and screaming until both sets of hawks return to the relative centers of their territories may be repeated every few hours throughout the day with several neighboring conspecifics. The chases consistently stop at the same locations, which we interpreted as the territorial boundaries.

The hunting behaviors of Red-tailed Hawks in the LEF also facilitate territory mapping. The almost constant updrafts, created by a northeasterly laminar flow of air against the Luquillo Mountains, allow Red-tailed Hawks to expend little energy while hunting in flight (Snyder and Snyder 1991). Thus, the majority of hunting occurs while in flight rather than from a perch (Snyder et al. 1987, Santana and Temple 1988).

We replicated earlier studies of Red-tailed Hawks in the LEF (Snyder et al. 1987, Santana and Temple 1988) by making visual observations of hunting Red-tailed Hawks and their interactions with conspecific neighbors and intruders from 5–20 January 1998, which is the onset of the nesting period in the study area (Snyder et al. 1987). We made our observations from many of the same overlooks used by Snyder et al. (1987) and Santana and Temple (1988). These consisted primarily of clear-viewing locations along roads, the top of rocks, slides, hillsides and escarpments, and the Mt. Britton and Yokahú lookout towers. Some of the previously-used road overlooks were no longer suitable due to vegetation changes. Fog precluded use of some of the high-elevation sites on some days, so we made the sampling from these lookouts a

priority when good viewing conditions prevailed. We began observations at about 0800 H and continued until 1700 H unless fog or rain developed. We recorded data directly onto photocopies of a 1981 1:20 000 U.S. Forest Service topographic map with 10-m contour intervals. We used the map copies to record observed flight lines for individual hawks, locations of perch points, copulation sites, nest sites, and locations of intraspecific interactions relative to obvious landmarks. We numbered observations sequentially and recorded observation times, vocalizations, details of individual birds' molts and markings, and the details of intraspecific interactions observed. We used fresh map copies each day and used additional map photocopies during the day as needed to maintain clarity of the records.

Due to the amount of time they spent in flight, hawks were easiest to detect initially when soaring aloft or when sunlight reflected off their wings as they circled. Hawks flying against the background of forest canopy were harder to locate and track visually. When we identified regularly-used perches, we subsequently could often locate perched hawks and observe them as they moved within their defended area. Once an individual hawk was sighted, we visually tracked the bird until it was lost from sight in clouds, the forest canopy, or behind topographical features. Hawks were in view for periods ranging from several minutes to an hour or more. When interactions between two or more Red-tailed Hawks occurred, each observer chose an individual or a pair to follow exclusively. Thus, it was advantageous to have multiple observers.

We easily plotted locations of perched hawks and points where hawks dove under the canopy. Apart from brief and intermittent cloud buildup and subsequent rain showers, sunlight was always available and we estimated locations of hawks flying within ca. 10 m of the forest canopy using the shadow they cast on the canopy. Errors of a few meters due to sun angle likely had only minor influence on our estimation of hawk locations. Observations were facilitated by the topography of the study area; we could accurately gauge a hawk's position and movements relative to cliff faces, drainage bottoms, and other topographic or landmark features of known size, elevation, and distance from the observation point. Finally, two observers frequently recorded data independently from different observation points. The resulting estimations of hawk locations were then compared between the two observers to verify the location plotted and improve the accuracy. In these ways, we were able to develop a sense of hawk size at different distances and make estimations of their location relative to the ground when they were soaring. Although some error undoubtedly occurred, we used methods identical to those used during the 1970s (Snyder et al. 1987) and 1980s (Santana and Temple 1988), so estimates should have equivalent bias and comparisons among study periods are valid. Based on the fact that we estimated visual locations against a topographically complex background at distances of only a few hundred meters, we suggest that our error is not substantially different from, and may be less than, error associated with radiotelemetry triangulations.

We used location points, flight lines, and behavioral observations to map the estimated area of each pair's

territory. We used ArcView 3.2 (Environmental Systems Research Institute, Inc.) to plot outermost location points for members of each Red-tailed Hawk pair onto a digital map of the study area. We then employed the ArcView Animal Movements extension (Hooge and Eichenlaub 1997) to calculate a 100% minimum convex polygon (MCP) territory size estimate for each pair. In the same manner, we created MCP home range size estimates of 11 Red-tailed Hawk territories mapped during the Snyder et al. study (H. Snyder unpubl. data) and of the 16 Red-tailed Hawk territories mapped by Santana and Temple (1984) to compare with our data.

We report means and standard errors for our calculations of territory sizes and overlap during each study period. We calculated the mean size for each territory that was used and also the proportion of the study area that comprised territories in all three periods. We used an analysis of variance to examine changes in territory sizes among the study intervals and an analysis of variance on ranks to examine changes in territorial overlap for those territories that were occupied consistently during all three studies. We used a paired *t*-test to examine differences in territory size among territories detected in the 1980s study and 1998, but not those detected during the 1970s because the defined study area was smaller.

We used a U.S. Geological Survey 30-m Digital Elevation Model (DEM) to characterize topographic features of each home range. Using ArcView Spatial Analyst (Environmental Systems Research Institute, Inc.), we derived slope and aspect grids for the study area. These grids were used to calculate mean elevation, slope, and aspect for each home range. Mean aspect was the circular mean (Fisher 1993). We also created a 10-m contour map of the study area. Using the ArcView XTools extension (Oregon Department of Forestry), we calculated the lengths of each 10-m elevation contour within each home range. We obtained a measure of topographic complexity by dividing length of contours by home range size. Our measure of topographic complexity was analogous to the Land Surface Ruggedness Index (LSRI) proposed by Beasom et al. (1983).

We used Pearson correlations and multiple regression to examine the relationship between elevation, slope, aspect, topographic complexity, and territory size. We used a Kruskal-Wallis test to determine if years could be pooled for further analysis. We tested for differences in mean aspect between years using Watson's Y_r test (Fisher 1993). All linear variables were examined for normality. Variables that were not normally distributed were transformed using natural log transformations. Principal components analysis (PCA) was used as a variable reduction method if independent variables were highly correlated. Several linear regression models were created. Mean aspect, a circular variable, was treated as a linear model with cosine (aspect) and sine (aspect) as the independent variables (Fisher 1993). For all regressions, territory size was considered the response variable. We used Akaike's Information Criterion (AIC) to select the best regression model (Burnham and Anderson 1998). Because we suspected that different features of the topography might have influenced territory size at different elevations, territories were divided into high and low elevation groups using 700 m as an arbitrary breakpoint to divide

the sample approximately in half. Regression models were reanalyzed in the manner described above using these two groups. All statistical analyses were conducted using SPSS for Windows 10.0.7 (SPSS, Inc.).

RESULTS

Our results were consistent with those from the previous studies in terms of both number of territorial pairs and the individual territorial boundaries. We obtained adequate territory data for 16 pairs of Red-tailed Hawks in the study area. Mean size of defended Red-tailed Hawk territories during our study was 124.3 ± 12.0 ha (i.e., 1 pair/1.24 km²). This was similar to our calculations of mean territory sizes of 139.0 ± 15.0 ha for 11 pairs from the 1970s study (Snyder unpubl. data) and 153.7 ± 15.8 ha for 16 pairs from the 1980s study (Santana and Temple 1984). Assuming territory size related to breeding density, the density of breeding pairs of Red-tailed Hawks in the LEF was at the high end of the range of nesting densities reported for the species in 10 different studies (1 breeding pair/1.3–24.9 km²; McGovern and McNurney 1986). In addition, there was substantial boundary overlap between defended territories. Territorial incursions by neighboring Red-tailed Hawks resulted in territory overlap that was greatest in the 1970s study ($\bar{x} = 27.3 \pm 8.8\%$), lowest in the 1980s study ($\bar{x} = 21.3 \pm 3.3\%$), and in between the two during our 1998 study ($\bar{x} = 24.3 \pm 4.2\%$), but these were not significant differences ($H_2 = 0.022$, $P = 0.989$).

In general, there was remarkably little temporal change in the spatial distribution, area, and boundaries of Red-tailed Hawks among the study periods (Figs. 1–3). Some territories, such as A and B, appeared to show slight increases and decreases among study periods (see Figs.). Other territories appeared to have disappeared altogether, but were replaced by new territories nearby. For example, territory I of the 1970s study (Fig. 1) may have shifted to become territory Q in the 1980s study (Fig. 2), but neither territory was occupied in 1998 (Fig. 3). Likewise, territory K in the 1970s study (Fig. 1) and K in 1998 (Fig. 3) may have also been R or P in the 1980s study (Fig. 2).

Nine territories (A, B, C, D, E, F, G, H, and J; Figs. 1–3) that were detected in all three study periods appeared to have been relatively consistent spatially. Although there were temporal fluctuations in the boundaries of these territories, over half of the area ($\bar{x} = 55.3 \pm 2.9\%$) within each

territory was common to that territory in all three studies. Furthermore, the territories did not temporally differ in sizes ($F_{2,24} = 0.726$, $P = 0.494$).

There were some territories not detected or mapped during the 1970s study, due to a more restricted study area than in the 1980s study or our 1998 study. Three of these (L, M, and O) appeared spatially similar between the 1980s and 1998 (Figs. 2 and 3). Territory N in the 1980s study (Fig. 2) appeared to have dissolved into two territories (N and T) in 1998 (Fig. 3). When pooling T into N for 1998, there was no significant difference in size between the 1980s and 1998 territories at locations L, M, N, and O ($t_3 = 0.065$, $P = 0.952$).

None of the linear topographic variables differed among years (Elevation, $\chi^2_2 = 2.384$, $P = 0.304$; Slope, $\chi^2_2 = 1.274$, $P = 0.529$; Topographic Complexity, $\chi^2_2 = 1.636$, $P = 0.441$; Aspect, $\chi^2_2 = 0.028$, $P = 0.986$); therefore, we pooled all years (Table 1). Territory size was transformed using the natural logarithm. All linear variables except elevation were negatively correlated with territory size (Elevation, $r = 0.041$, $P = 0.793$; Slope, $r = -0.401$, $P = 0.008$; Topographic Complexity, $r = -0.406$, $P = 0.007$). Slope and topographic complexity were strongly correlated with each other ($r = 0.994$, $P < 0.001$); therefore, they could not be used as independent variables in the same regression model. A new variable was created based on component I of the PCA used to combine slope and topographic complexity. Because of the extremely low correlation of elevation and territory size, elevation was not used as an independent variable in any regression model.

Seven regression models were tested. Models 1–3 were single-variable linear regressions of slope, topographic complexity, and the PCA variable, respectively. Model 4 was a linear regression with cosine (aspect) and sine (aspect) as the independent variables. Models 5–7 were all possible pair-wise combinations of the four topographic variables.

Size of territory was not independent of slope and aspect. Territory size decreased as slope increased. Generally, the smallest territories had aspects facing southeast. The model with the best data fit predicts territory size using the formula:

$$\text{Territory size} = e^{5.6762 - 0.038 \text{ Slope} + 0.1395 \text{ Cosine (Aspect)} - 0.1404 \text{ Sine (Aspect)}}$$

The slope-aspect model received the smallest AIC value, and the best single-variable model was based on topographic complexity. The topographic vari-

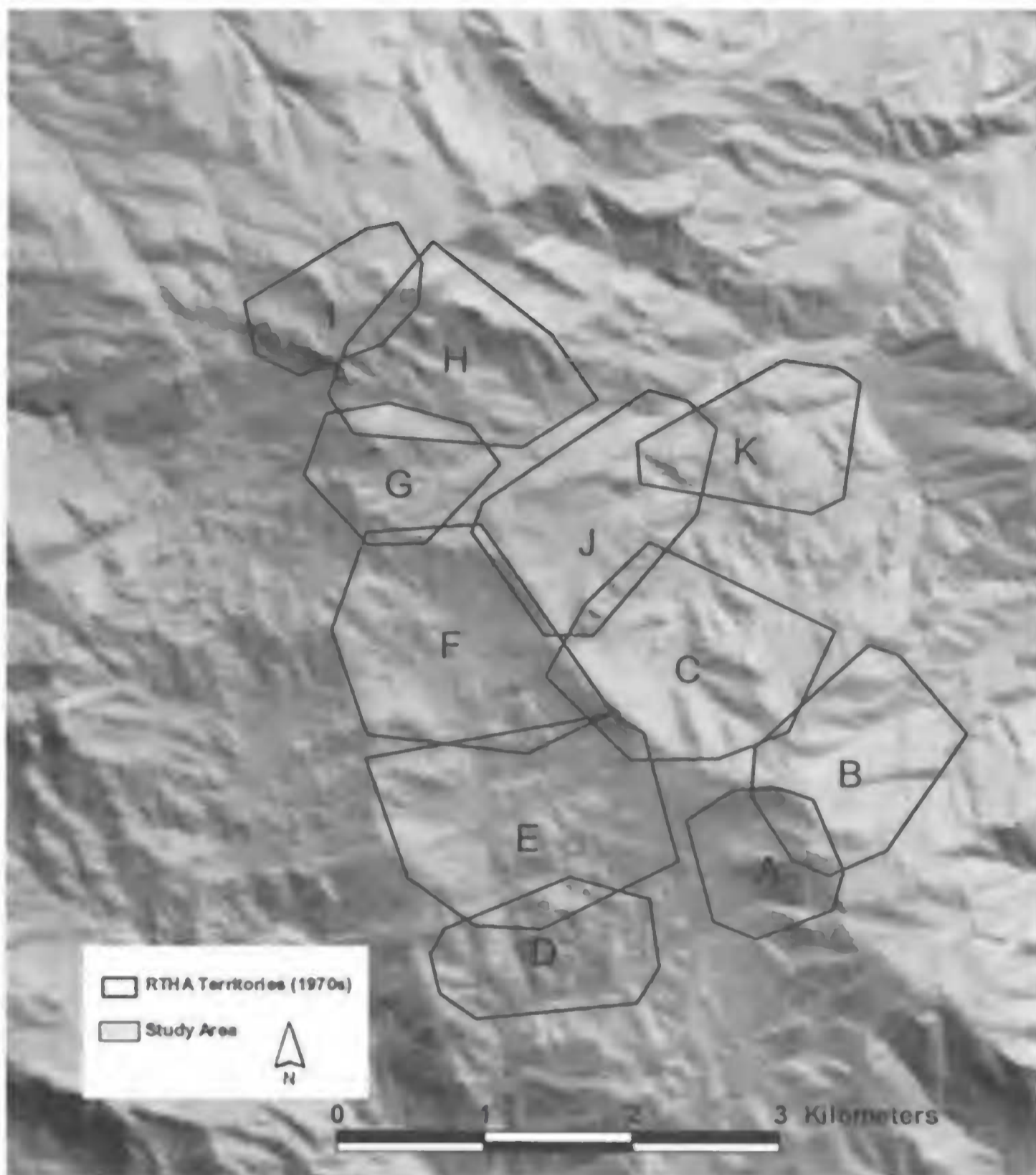


Figure 1. Estimated spatial distribution of Red-tailed Hawk (RTHA) territories in the Luquillo Experimental Forest, Puerto Rico, during the early 1970s (H. Snyder unpubl. data).

ables that influenced territory size varied by elevation. Low-elevation territories were most influenced by aspect and topographic complexity. High-elevation territories were most influenced by aspect.

DISCUSSION

We suspect the temporal and spatial stability of Red-tailed Hawk territories in the LEF might be related to the hawks' apparent use of permanent geographic features such as hilltops and ridgelines

to delineate territory boundaries and corners. These geographic features might serve an important function by funneling the updrafts from the tradewinds. This allows Red-tailed Hawks on the east and northeast sides of the highest peaks and ridgelines to soar or hover in the strong updrafts, from which they can hunt and defend any part of the territory with a minimum expenditure of energy. In addition, the relatively constant updrafts allow the Red-tailed Hawks to be on the wing from pre-dawn to twilight. This is especially true at high-

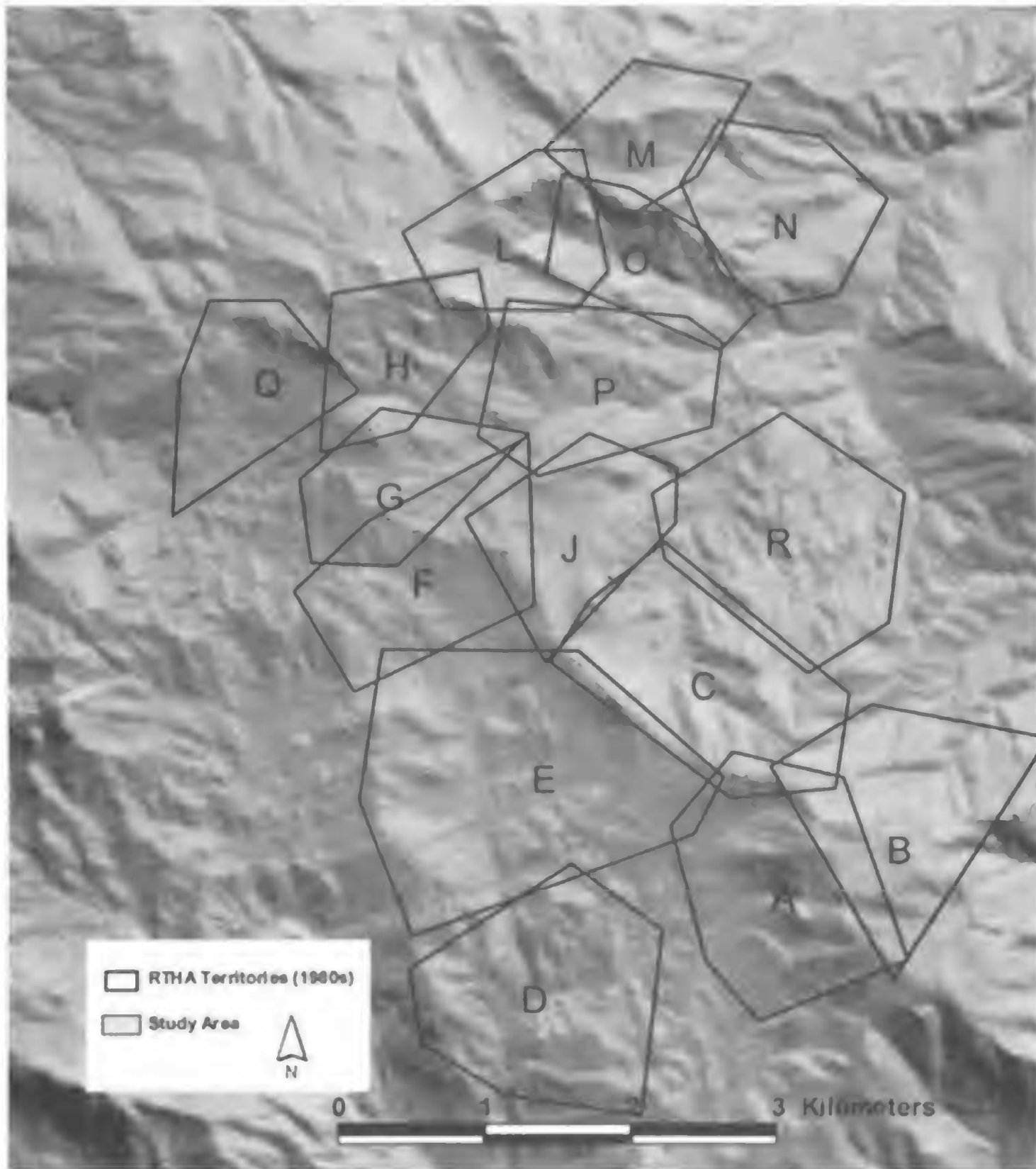


Figure 2. Estimated spatial distribution of Red-tailed Hawk (RTHA) territories in the Luquillo Experimental Forest, Puerto Rico, during the early 1980s, based on Santana and Temple (1984).

er elevations where the updrafts should be stronger. Thus, the hawks are not constrained by time of day, as is the case in areas where soaring is dependent upon thermal updrafts. For example, Red-tailed Hawks occupying areas on the lee side of ridges usually gained and maintained altitude by extended flapping and circling rather than soaring.

The role of topographic complexity in territory size is difficult to interpret. Increasing complexity

may create more regions within a given territory in which updrafts occur, resulting in more areas in which a hawk can efficiently soar. Topographic complexity may also indicate a greater surface area within a territory than would be estimated by the MCP estimate, which is based on a flat surface area. However, we found a very high correlation between slope and topographic complexity. This might indicate that the LSRI method (Beasom et al. 1983) of measuring topographic complexity is

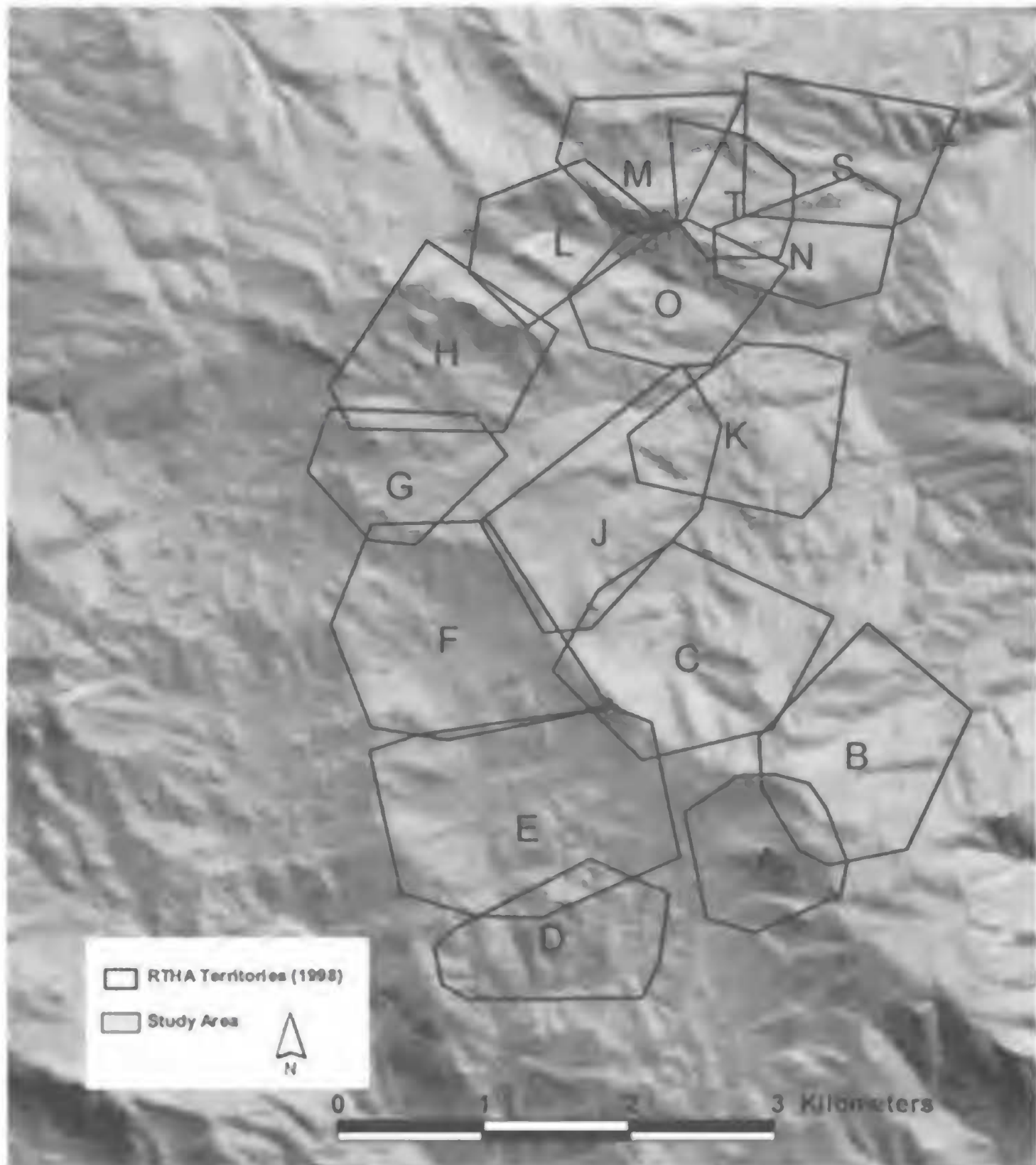


Figure 3. Estimated spatial distribution of Red-tailed Hawk (RTHA) territories in the Luquillo Experimental Forest, Puerto Rico, during January 1998 (this study).

overly sensitive to slope, conveying little additional information about the area.

There appeared to be little variability in territorial boundaries and areas among the three studies, despite a passage of 26 yr and forest damage associated with Hurricane Hugo in 1989. The hurricane struck the LEF study area with 4 hr of winds reaching as high as 227 km/hr (Scatena and Larsen 1991). Resulting damage to the forest was deemed so severe that forest composition and dy-

namics were affected for several years (Brokaw and Grear 1991). Removal of canopy trees by the hurricane resulted in numerous openings in the forest canopy (Brokaw and Grear 1991, Scatena and Larsen 1991, Waide 1991). Openings in the canopy might have facilitated hunting by Red-tailed Hawks and, although there are no supportive data, might have resulted in an increase in Red-tailed Hawks in the LEF. If any increase occurred, however, it was likely short-lived, as the Red-tailed Hawk den-

Table 1. Mean elevation (m), slope and aspect (degrees), and topographic complexity (m/ha) of Red-tailed Hawk territories, Luquillo Experimental Forest, Puerto Rico. Data derived from 1972–75 (Snyder et al. 1987), 1981–83 (Santana and Temple 1984), and 1998 (this study) were pooled.

VARIABLE	MEAN	STAN-	MINI-	MAXI-
		DARD		
		ERROR	MUM	MUM
Elevation	671.1	23.2	300.9	956.0
Slope	19.5	0.6	12.8	28.2
Aspect	107.1	14.4	12.0	289.0
Topographic complexity	395.5	12.3	269.0	583.8

sity in 1998 was not different than the pre-hurricane density (Santana and Temple 1984, Snyder et al. 1987).

The 1970s study (Snyder et al. 1987) and 1980s study (Santana and Temple 1984) did not report the number of days of Red-tailed Hawk observation. However, it is obvious our study of 15 days was quite limited in duration compared to these earlier investigations. The differences we found in some territory boundaries might be attributable to the time constraints of our study compared to the earlier studies (Santana and Temple 1984, Snyder et al. 1987), and that our survey was conducted in January, which is at the start of the nesting cycle for resident Red-tailed Hawks and when they are presumably most aggressive in territorial defense (Snyder et al. 1987). However, there was no statistical difference in the territory sizes or boundary overlap among the study periods. Thus, we believe our data accurately depict territory sizes, boundaries, and Red-tailed Hawk density at the onset of the 1998 breeding season.

There appeared to be a number of individual Red-tailed Hawks that were unattached to a mate or territory passing through the study area and they traversed the defended territories by maintaining high altitudes. Territorial residents would occasionally soar upward, but remained below the intruder as it passed over the area. As the intruder approached a boundary, the adjacent resident Red-tailed Hawks would rise up toward the intruder. In this way, a high-altitude intruder would be “escorted” across the study area by each successive pair of resident hawks. These encounters appeared to be non-aggressive as long as the intruder maintained a high altitude and continued moving

across the area. Only when an intruder began descending or circling were chases initiated. None of the high-altitude intruders were observed diving into known territories. Rather, they invariably “vanished” into the distance after having passed over several occupied territories. Therefore, we assumed that these intruders were not, in fact, adjacent or distant neighbors who were cruising above the landscape. In addition to an unknown number of adult Red-tailed Hawks that flew over the territories, we observed at least two immature Red-tailed Hawks that appeared to be living inconspicuously among the territories in the study area. Immature Red-tailed Hawks were rarely observed soaring. Rather, they were observed moving low above the canopy of the forest, and they quickly dove out of sight into the canopy when detected and pursued by a resident.

Territorial behavior among birds can lead to generally even distribution of individuals within a population (Newton 1998). High site-fidelity among individuals in a population might lead to relatively long-term spatial stability of territory areas. Furthermore, stability of a population over several years suggests that densities might be limited by competition for territorial space (Newton 1991). Our data, combined with that of Santana and Temple (1984) and Snyder et al. (1987), suggest there was a high degree of temporal stability in the density and spatial distribution of Red-tailed Hawks in the LEF that may be linked to geographic features. Furthermore, the temporal stability of the spatial distribution of Red-tailed Hawk territories in the study area leads us to believe the area is at or near saturation.

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